

# THE STRUCTURAL EVOLUTION OF THE BIVALVE SHELL

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**ABSTRACT.** Direct study of the course of evolution of bivalve shell structures has been prevented by the lack of well-preserved lower Palaeozoic material. The 'primitive' molluscan shell structure probably consisted of an outer aragonitic prismatic layer, the prisms being polygonal in transverse and columnar in longitudinal sections. The middle and inner shell layers consisted of nacreous structures. Morphologically similar structures are produced inorganically from the solidification of metals containing impurities. It is suggested that the prism/nacre combination originally arose spontaneously as a result of the precipitation of calcium carbonate with protein (impurity). The subsequent elaboration of the shell structure combinations took place along seven major morphological trends. The main structural changes have been: the modification and loss of the outer prismatic layer; the elaboration of the middle layer from nacre into various other types of dendritic growth such as calcitic foliated or aragonitic crossed-lamellar structures; and the loss of organized structure to produce a homogeneous granular structure. In all the series there has been a progressive loss of layers from the 'primitive' three to a more 'advanced' two or even one.

In recent years there has been considerable interest in the calcified structures of invertebrates and the structure of the molluscan shell, particularly that of the Bivalvia, has received much attention (Bøggild 1930; Taylor *et al.* 1969, 1973; Wise 1970, 1971). It is now known that the shells consist of a number of distinct structures and the micro-morphology and distribution of these structures amongst the various taxa is becoming well known. Although the arrangement of the structures in each of the bivalve superfamilies is obviously related to their phylogenetic history, it is difficult to see how the various structures are related to each other and how they might have evolved. Whilst it has been possible to study the shell structure of some fossil bivalves, the preservation problems caused by the usually aragonitic shells have meant that except in very few cases it has not been possible to extend these studies very far back into the Palaeozoic. This is in contrast to the Brachiopoda, where the frequently good preservation of the calcitic shell has enabled the shell structure of Cambrian forms to be examined (Williams 1968). This lack of information from the lower Palaeozoic is particularly unfortunate because many bivalve lineages are of considerable antiquity and it seems that most of the major radiation of shell structure types took place in the Ordovician (Pojeta 1971).

If it is accepted that the Bivalvia are a monophyletic group, then all of the shell structure types observed in Recent bivalves must have evolved from a single shell structure combination. A study of the distribution of shell structures in all living superfamilies (Taylor *et al.* 1969, 1973) included the discovery of some transitional combinations, which, together with evidence of relationships derived from other available characters makes possible the tentative presentation of an attempt to demonstrate the course of evolution of bivalve shell structures. The original stimulus for this idea was the discovery of a metallurgical analogy (described below) which even if not directly applicable to calcification in bivalves, at least provides a model which (to the author at least) has made the relationships of the various shell structures comprehensible.

## THE SHELL STRUCTURES

The various bivalve shell structures have been described in detail by Taylor *et al.* 1969, Wise 1970, 1971, and only the main points relevant to this paper are discussed below.

*Prismatic structures*

Simple prismatic structures, whether calcite or aragonite have been shown by various workers (Taylor *et al.* 1969) to resemble the group growth of spherulites seen in inorganic samples (Grigor'ev 1965). Recent further work has shown the spherulitic nature of the first calcification on the periostracum surface (Pl. 60, figs. 1 and 2). Although the crystallographic *c* axis is generally parallel to the long axis of the prisms, the alignment is not always exact and each of the small crystallites making up the prism has a slightly different orientation, usually divergent from the morphological long axis. In some species the arrangement of the crystallites may be fanlike.

The composite prismatic structure has the longest morphological and the crystallographic *c* axes aligned more or less parallel to the outside of the shell, but in many respects closely resembles the simple prismatic structure.

*Nacreous structures*

Sheet nacre consists of tablet-shaped crystallites laid down in laminae; the crystallographic *b* axis of the tablets is generally oriented in the growth direction of the shell and the *c* axis is normal to the plane of the tablet. Areas of nacre appear to behave as a single crystal and the crystallites link up to produce large dendritic growth patterns (text-fig. 1). Often large growth spirals are formed arising from screw dislocations (Wada 1961). In columnar or lenticular nacre (Taylor *et al.* 1969; Wise 1970) the tablets are arranged into columns, the growth axis of the columns corresponding to the *c* axis of the aragonite. These columns apparently arise by screw dislocations at the growing tip (see Erben 1971, p. 59, pl. 2, fig. 5) and are another form of dendritic growth.

*Foliated structure*

This structure is always composed of calcite and consists of long lath-like crystallites arranged in side-to-side contact and into overlapping sheets. In general the crystallographic *c* axis is aligned in the growth direction but local differences in alignment of areas of crystallites are common. This structure has long been considered as dendritic growth (Watabe and Wilbur 1961) and as shown in Pl. 60, fig. 4, this interpretation is reasonable.

*Crossed-lamellar structure*

This is one of the most common shell structures. It consists of elongate needle-like crystallites which are arranged into lamellae. In adjacent lamellae the morphological alignment of the crystallites differs by about  $98^\circ$ . The crystallographic *c* axis lies within the plane of each lamella, but the orientation of the *c* axis varies by approximately  $8-10^\circ$  between adjacent lamellae. Although the structure shows strong



TEXT-FIG. 1. Dendritic growth pattern of aragonite nacre crystallites on the inner surface of the inner layer of *Neotrigonia dubia*. Traced from electron-micrographs,  $\times 9000$ .

superficial resemblance to twinning there is no evidence of any twin relationship between the lamellae. Each of the two orientations shown by crystallites in the lamellae show complex branching patterns (text-fig. 2) and it is possible that some sort of dendritic growth mechanism is operative. Much work on the mode of secretion of this structure, similar to that on prisms by Nakahara and Bevelander (1971) is needed.

#### *Complex crossed-lamellar structure*

This structure appears genetically related to crossed-lamellar structure and can probably be best thought of as being the intergrowth pattern resulting from crossed-lamellar structure in two alignments at right angles to each other. As a result there are four orientations of crystallites. Occasionally the texture resembles that of the patellacean gastropods, interpreted as spherulitic by McClintock (1967).

#### *Homogeneous structure*

This is a name given to a fine-grained structure with no particular crystal form; it can be



TEXT-FIG. 2. Tangential section of the outer crossed-lamellar layer of *Hippopus hippopus* showing the dendritic nature of each of the lamellar orientations. Traced from photomicrographs.

derived from any of the other shell structures by a diminution in grain size and a breakdown of structural arrangements. Further detailed study will probably reveal different types of homogeneous structures but these are not yet apparent.

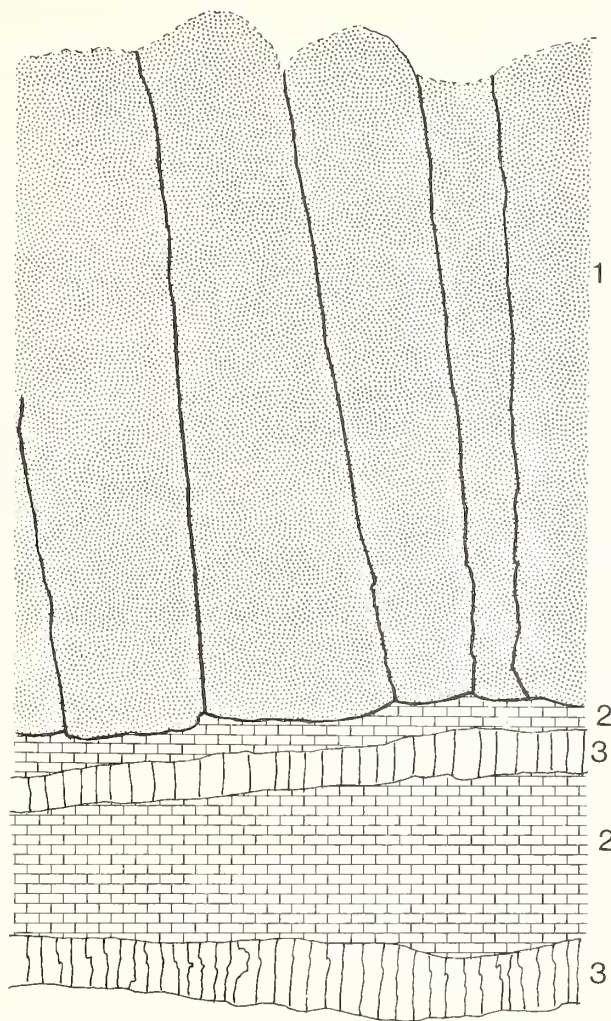
#### *Homologies between layers*

Although homologies between shell layers from various taxa should be made with caution (Taylor *et al.* 1969) it is reasonable in most cases to use the trace of the pallial myostracum as a marker horizon. This separates the inner from the middle and outer layers or just the outer layer, depending on how many layers are present. In some Pteriomorphia the pallial myostracum is absent and in others it represents secondary pallial attachment and thus great care must be taken if homologies are attempted between this group and the rest of the bivalves.

#### *The 'primitive' shell structure*

Before discussing the evolution of the bivalve shell structure it is necessary to attempt to establish the nature of the 'primitive' shell structure. McAlester (1965, 1966) has demonstrated, mainly through the evidence of pedal muscle scars, how the bivalve *Babinka* may be derived from a monoplacophoran ancestor. At the time, McAlester thought that this may have been a special character of the Lucinacea and he suggested a polyphyletic origin for the bivalves. However, it is now known that several other bivalve groups may be similarly derived from a monoplacophoran ancestor (N. J. Morris, pers. comm.) and the monophyletic derivation of all bivalves from this source is a reasonable proposition. It would thus seem reasonable to regard the structure of the Monoplacophora as being the ancestral structure to that of the Bivalvia. The work of Schmidt (1959) and Erben *et al.* (1968) has shown that, with the exception of *Tryblidium*, the shell structure of Monoplacophora is, and was, aragonitic and consisted of an outer simple prismatic layer and nacreous inner layers (text-fig. 3). The prisms of the outer layer lie with their long axes normal to the outer shell surface, are polygonal in horizontal section, and bounded by a sheath of protein matrix (see also figs. 1-8 in Menzies 1968). The inner nacreous layer is divided by a thin sheet of blocky prisms such as are normally secreted beneath muscle attachment areas. Another sheet of these prisms occurs on the innermost part of the shell. Similar sheets of myostracal prisms have been described from the inner shell layer of some Mytilacea (Taylor *et al.* 1969, pl. 25, fig. 2) and it was suggested that they were formed during times of temporary attachment of the mantle to the shell.

Several bivalve superfamilies have a structural combination of aragonite simple prisms with inner and middle nacreous layers. Although the number of living superfamilies having this combination is only five out of thirty-nine, they usually belong to lineages which extend far back into the Palaeozoic, whereas many of the other superfamilies not having this structure have arisen in the late Palaeozoic or Mesozoic. The superfamilies having this 'ancestral' condition are the Pholomyadacea, Pandoracea, Poromyacea, Unionacea, and Trigonacea. Moreover the combination of calcite prisms and nacre, as found in the Pteriacea, Pinnacea, Mytilacea, and Ambonychiacea (extinct) which all originated in the Palaeozoic, is not very different. It has often been stated that the Nuculacea show the most 'primitive' structure (Oberling 1964), but it will be shown later in this paper that it represents an early modification.



TEXT-FIG. 3. Section through shell of *Neopilina galathea* Lemche. Traced from Erben *et al.* (1968, pl. 3). 1 = simple prisms; 2 = nacre; 3 = myostracal prisms.

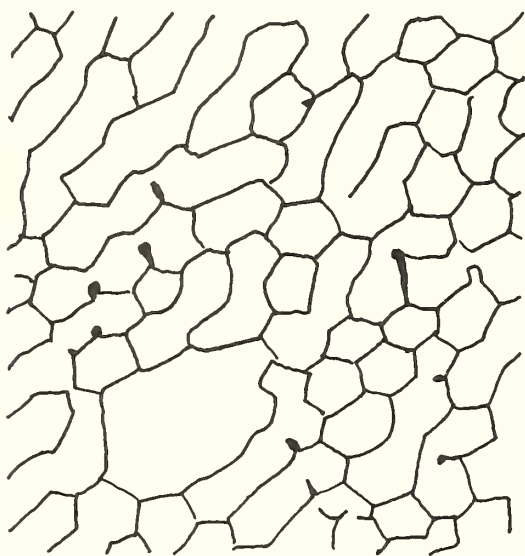
Other evidence of the 'primitive' nature of the simple prisms and nacre combination is seen in its occurrence in the Archaeogastropoda (Wise 1970; Erben 1971; Taylor unpub.) in *Nautilus* and ammonites (Grégoire 1962; Mutvei 1964; Erben *et al.* 1969). In these groups the simple prisms are not as well defined as in the Bivalvia but their spherulitic nature is clear. The nacreous layers usually consist of columnar nacre.

The 'primitive' shell structure may thus be fairly reasonably defined. Assuming a monophyletic origin for the Bivalvia, the problem is how have all the other shell structure combinations arisen from this 'primitive' combination? There is apparently little similarity between the more advanced crossed-lamellar and complex

crossed-lamellar shells and the primitive nacreo-prismatic forms and after some years' consideration of the problem no link could be seen. The situation was changed by the discovery of a metallurgical analogy which caused a reorientation of thought resulting in the present tentative proposal of an evolutionary series of shell structure combinations. This does not mean that the metallurgical analogy is suggested as the mechanism for calcification in bivalves but merely that its consideration has been instructive. A model need not be correct to be useful.

#### THE CELL-DENDRITE ANALOGY

During the solidification of impure melts in quiescent conditions microsegregations of the impurity may occur. A microstructure which often arises is that of cellular structure, where at the growth surface most of the impurity segregates into



TEXT-FIG. 4. Cellular impurity structure as found in metals. Traced from Chadwick (1967, figs. 4-6(d)).

the walls of a polygonal cell structure (text-fig. 4) (Chalmers 1958). In section the cells are columnar and the impurity appears as a thin line separating adjacent cells (Chadwick 1967). This microstructure may arise if there is a zone of constitutional supercooling (i.e. supercooling developed as a result of compositional changes in the liquid during freezing) at the solid/liquid interface. The usual explanation of the development of the cellular structure (Chalmers 1958; Tiller 1963; Chadwick 1967) is that small irregularities of the solid protruding into the supercooled liquid grow faster than the surrounding solid; the protuberances reject impurities in directions both normal to the tip and laterally. If this process occurs over the entire solid/liquid interface then eventually a hexagonal structure will be produced. The stages in the

development of the cell structure show a progression from a planar interface to a 'pox' structure, then elongate cells and finally regular polygonal cells (Tiller 1963).

If the speed of crystal growth is increased, the temperature gradient decreased (Chalmers 1958) or the degree of constitutional supercooling increased (Chadwick 1967), then the cellular structure may break down into dendritic growth. The criteria for dendritic growth are that the crystals should be branched or that the axis of the growing domain should coincide with a crystallographic axis (Chalmers 1958).

It is uncertain how far this analogy can be taken with reference to shell microstructure, but there are obvious resemblances between this metallurgical example and the microstructure of simple prisms (cells) and nacre (dendrites). There does

not seem to be any reason why the precipitation of calcium carbonate with an impurity (organic matrix) should not produce similar structures, perhaps for similar reasons. The hypothesis put forward here is that the microstructure of simple prisms and nacre corresponding to cells and dendrites originally arose spontaneously as a consequence of the precipitation of calcium carbonate contemporaneously with organic matrix under a certain set of physico-chemical conditions. Subsequently, because of some selective advantage in this structural combination, perhaps strength (Taylor and Layman 1972), this arrangement became stabilized. Further elaboration of the depositional conditions resulted in the formation of the other shell structures, such as foliated or crossed-lamellar structures, both of which appear to have dendritic growth patterns. These are both in a position homologous with the middle nacreous layers and could arise by changes in the dendritic growth patterns of the nacreous structure. The elaboration of shell structures took place at different rates and in different ways in various groups of bivalves. The details of these changes are discussed below.

#### EVOLUTIONARY TRENDS IN SHELL STRUCTURE COMBINATIONS

The evidence for the evolution of the various shell layer combinations was obtained by superimposing shell structure data upon a phylogeny derived from all available characters and geological history (Taylor *et al.* 1973, fig. 33). It has been possible in this way to demonstrate seven separate trends in shell structure evolution; these are shown in text-fig. 5. Examples of living taxa having a particular structural combination in each series are indicated. The trends and examples are not phylogenetic lineages but represent possible morphological grades arranged in order of increasing advancement.

As previously stated some superfamilies are relatively little altered from the ancestral condition; these include the Pholadomyacea, Unionacea, Trigonacea, some Pandoracea, some Poromyacea, and the early shell of the Clavagellacea.

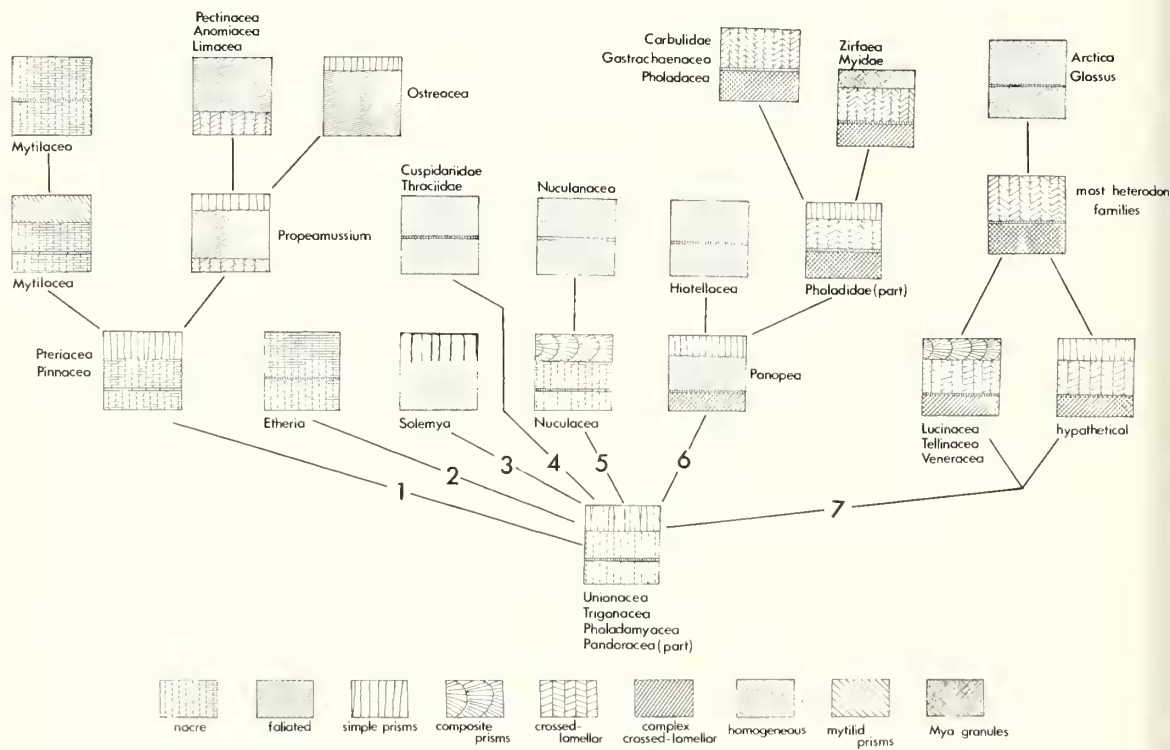
##### *Trend 1*

The first step in this sequence (text-fig. 5) was that the outer, simple prismatic layer, aragonite in the ancestral condition, became calcite; this state is found today in the superfamilies Pinnacea, Pteriacea, and in the extinct Ambonychiacea. Although there has been much research into the calcite-aragonite problem in molluscs (Lowenstam 1954, 1964; Dodd 1963; Hall and Kennedy 1967; Kennedy *et al.* 1969) we still know very little about how and why an organism can produce aragonite, or calcite, or both, in the same shell. The temperature effect originally proposed by Lowenstam (1954) has so far only been successfully demonstrated in *Mytilus* (Dodd 1963); other examples are of doubtful validity (Kennedy *et al.* 1969; Taylor *et al.* 1969). The only generalizations one can make are that bivalves which normally employ a calcitic outer layer are all epifaunal and the slightly lower solubility of calcite may have some advantage in this situation. This is not to say that a temperature effect does not exist but that it is *non proven* in most cases.

An early divergence of this trend may have been to the Mytilacea where the outer calcitic prisms are very fine, needle-like, and inclined towards the shell margin.

A possible mode of formation of similar structures in mammalian enamel has been proposed by Osborn (1970). A further development in this series was the loss of the outer calcitic prismatic layer to leave the two underlying nacreous layers. This condition is found in some tropical Mytilacea (Hudson 1968; Taylor *et al.* 1969) and has been related to a temperature effect.

Another offshoot from the calcite prisms/nacre combination gave rise to the sequence which includes the Pectinacea and Ostreacea. The probable first stage in evolution was the transformation of the middle nacreous layer to foliated structure which is calcite, i.e. one type of dendritic growth to another. The changes in microstructure accompanying this transformation may merely be a result of the mineralogical change rather than any direct genetic effect upon shell structure. Although the initial causes of the change are unknown, there are some mechanical properties of the foliated shell, such as the resistance to fracture under impact, which may have some selective advantage (Taylor and Layman 1972). It is uncertain whether the condition found in oysters of calcite prisms (right valve only) and foliated structure, is more 'primitive' or 'advanced' than the combination found today in *Propeamussium* of calcite prisms, foliated structure and a thin crossed-lamellar layer. However, the combination found today in the Pectinacea, Limacea, and Anomiacea of foliated structure and crossed-lamellar structure is a further development from



TEXT-FIG. 5. Diagram showing the postulated evolutionary radiation of shell layers into seven major trends from the ancestral 'primitive' condition. The names in the trends represent living taxa having the particular shell structure combination. The series do *not* necessarily imply a phylogeny.

the 'Propeamussium' condition involving the complete loss of the outer prismatic layer. In most of the Ostreacea the outer prismatic layer is found only as a very thin layer on the upper valve; in the Pycnodontidae it is absent altogether. It seems more likely that the oyster structure is a development from the 'Propeamussium' condition by the loss of the inner crossed-lamellar layer.

#### *Trend 2*

This is a simple case merely involving the loss of the aragonitic, outer, simple prismatic layer, leaving nacreous structure as the outer layer. This condition is found today in the oyster-like unionacean *Etheria*.

#### *Trend 3*

This sequence is again little changed from the ancestral condition and is found today only in *Solemya*, in which the outer layer consists of simple aragonite prisms and the inner of a very thin homogeneous layer. The prisms of the outer layer are very irregular and have thick interprismatic walls. The prism outlines at the growth surface are frequently elongate and irregular. The inner homogeneous layer is very thin and is probably derived from the structural breakdown of nacreous structure.

#### *Trend 4*

In this series the end members are represented today by the Cuspidaridae and the Thracidae; in both of these families the shell consists almost entirely of homogeneous layers. It is fairly certain that both of these groups have descended from a prismato-nacreous ancestor and certainly in the Cretaceous some *Thracia*-like bivalves have a prismato-nacreous shell. A possible transitional stage is seen in the Recent *Poromya granulata* in which the outer layer is now homogeneous, but the two inner layers are nacreous. Perhaps a last vestige of prismatic structure is seen in Recent *Thracia*, where although most of the shell is homogeneous, the very outermost part of the outer layer shows spherulitic structures resembling the initial stages of a prismatic layer (Pl. 60, fig. 3).

#### *Trend 5*

In this sequence the simple prismatic layer changes to the composite prismatic layer such as found in the Nuculacea. This change is apparently a fairly simple one involving merely the development of a reflected mantle margin, causing the prisms to become aligned parallel with the outside of the shell rather than normal to it (text-fig. 5). This may have happened as a result of the development of the marginal denticles characteristic of the Nuculacea, which probably allow better valve closure against predators. The Nuculanacea were probably derived from a *Nucula*-like ancestor, but at the present day they have a two-layered shell, both layers consisting of homogeneous structure. However, a Jurassic nuculanid *Ryderia graphica* has a shell structure of composite prisms and nacreous structure similar to that of the Nuculacea (Cox 1959; Taylor *et al.* 1969). The change probably consisted of the loss of the outer layer and the breakdown of the two nacreous layers to homogeneous structure.

### Trend 6

In this sequence the first stage we see is that represented today by *Panopea* and the evidence from this genus has been of key importance in the interpretation of the evolution of shell layers. *Panopea* has an outer aragonitic simple prismatic layer (albeit irregular), a middle homogeneous layer, and, within the pallial line, an inner layer which is sometimes homogeneous but at other times may be built from spherulite-like structures, resembling complex crossed-lamellar structure. A further modification of this series along one offshoot is the loss of the outer prismatic layer leaving a shell consisting of two homogeneous layers as in *Hiatella* and *Panomya*.

Another divergent trend resulted in the development of a middle crossed-lamellar layer with the retention of the outer, simple prismatic layer; this condition is found in some Pholadacea. The inner layer may consist of homogeneous or complex crossed-lamellar structure. In other Pholadacea and the Gastrochaenacea, the outer simple prismatic layer has been lost and the shell consists of crossed-lamellar and complex crossed-lamellar layers.

In *Mya*, *Platydont*, and *Zirfaea* the outer layer consists of a grey, granular structure which may be derived from a modification of the outer simple prismatic layer but this is not certain. The other layers are as in the Pholadacea.

### Trend 7

This sequence contains, with the exception of the Myoida, all of the rest of the heterodont bivalves, which are by far the most numerous of Recent bivalves. However, more problems are posed in this sequence than in any other, the main difficulty being that no transitional structures such as those of trend 6 have been found. Thus, we are left with rather a large discontinuity between the ancestral structures and what is considered the most 'primitive' structural combination in the sequence. However, as possibly similar changes have taken place in trend 6, there is no reason to suppose that they may not have taken place in this one. In accordance with the sequence of events in trends 5 and 6 we may suppose that the three-layered shell consisting of composite prisms, crossed-lamellar, and complex crossed-lamellar structures might be the most 'primitive' condition now seen in this sequence. This particular combination is found today in the Lucinacea, Tellinacea, and some Veneracea; of these the Lucinacea are an ancient superfamily and can be followed through the Babinkacea back to the lower Ordovician (McAlester 1965). Included at this

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#### EXPLANATION OF PLATE 60

Fig. 1. Inner surface of the periostracum and edge of prismatic layer in *Anodonta cygnea* showing the initial spherulites (arrowed) on the periostracum surface. The spherulites increase in size and eventually impinge to form the polygonal outlines of prismatic structure. Scanning electron-micrograph,  $\times 550$ .

Fig. 2. As Fig. 1, but detail of an individual spherulite showing the structure of fine radiating needles.  $\times 1300$ .

Fig. 3. Initial spherulites in the outermost part of the outer layer of *Thracia phaseolina*. This is all that remains of prismatic structure in this family. Scanning electron-micrograph,  $\times 1100$ .

Fig. 4. Polished, etched section of foliated structure of *Pecten maximus*, showing the dendritic nature of the folia growth. Acetate peel,  $\times 150$ .



1



2



3



4

TAYLOR, structure of bivalve shell

level is a hypothetical structural combination similar to that described above, but with an aragonite simple prismatic outer layer rather than a composite prismatic one. This has never been found in any fossil or living bivalve, but the evidence from trend 6 suggests that it may once have occurred in trend 7. In trend 5 the derivation of composite prisms from simple prisms by changes in the shape of the shell margin has been discussed.

As in the other trends the next stage in the evolutionary sequence from the most primitive observed is the loss of the outer prismatic layer, whether it be composite or simple, to form a two-layered shell consisting of crossed-lamellar and complex crossed-lamellar structures. This structural combination is found in many heterodont bivalve superfamilies such as the Carditacea, Crassatellacea, Chamacea, Cardiacea, Mactracea, etc., and also in the Arcacea and the Limopsacea, both at present classified in the Pteriomorphia. A further development is the breakdown of the crossed-lamellar and complex crossed-lamellar structures to form homogeneous structure. This may occur in one or both layers and many minor variations (not illustrated here) are found, particularly in the Veneracea (Taylor *et al.* 1973, text-fig. 18). A totally homogeneous shell is found in the Gaimardiacea and some Arctica-cea (*Arctica* and *Calypptogena*).

#### DISCUSSION

In the evolution of the various structural series three main types of structural change have probably taken place. These may be: (a) loss of layers, (b) orientation changes, (c) complete structural changes.

(a) *Loss of layers.* This is the most commonly occurring of the structural trends and occurs in all of the recognized sequences, the main consequences being the reduction in the number of shell layers from a 'primitive' three to a more 'advanced' two. This usually involves the loss of the outer prismatic layer, whether formed from composite or simple prisms. In some sequences inner layers may be lost, for example in trend 1, but this is apparently associated with changes in the position of pallial attachment to the shell.

(b) *Orientation changes.* The only major example of this type of change is the formation of composite prisms from simple prisms by changes in the shape of the shell margin as discussed above.

(c) *Complete structural changes.* Other more major changes may arise as a result of mineralogical transformation such as the change from aragonitic nacre to calcitic foliated structure, as seen in trend 1. The differences in structure observed may be merely a result of the fact that trigonal calcite will not produce the same crystallization structures as orthorhombic aragonite, rather than there being a major change in the secretory regimes. Both nacre and foliated structure are regarded as types of dendritic growth form.

The origin of crossed-lamellar and complex crossed-lamellar structures and their appearance in the various morphological trends is much more difficult and no sensible explanation can be provided with present knowledge. What is certain is that crossed-lamellar structure arose in a position homologous with the middle nacreous layer of the 'primitive' condition. We have no surviving intermediate stages in the

transformation, but crossed-lamellar structure appears to be a form of dendritic growth and might be derived by an elaboration of nacre dendrites. Similarly, the formation of complex crossed-lamellar structure is also not understood, but it has evolved in a position homologous with the inner nacreous layer of primitive forms. (Dr. Donald Boyd (University of Wyoming) has recently found what appear to be transitional stages in *Schizodus*, in which a crossed-lamellar layer is present in the middle of an otherwise prismatic-nacreous shell.)

Various mechanisms could be invoked to explain the formation of crossed-lamellar structure including: type and composition of the organic matrix, physico-chemical conditions in the extra-pallial fluid, piezo-electric effects, or an alternating electric charge at the valve margins. None of these suggestions has, as yet, any experimental support. Workers adhering to the template theory of calcification would stress the importance of compositional differences in the shell matrix as evidence.

One of the most widely recurring of the morphological changes is the apparent breakdown of distinct crystalline morphology to form homogeneous structure. This structure can arise from simple prisms, composite prisms, crossed-lamellar, complex crossed-lamellar, and nacreous structures, with, in each case, a morphologically similar result, that is a fine-grained, irregularly granular structure. The reasons for this structural change are again not readily apparent, but speed of crystallization may be responsible; growth may be more rapid in homogeneous shells.

One feature obvious from text-fig. 5 is the independent origin of crossed-lamellar structure in several unrelated groups of bivalves; it occurs in the Pectinacea-Limacea-Anomiacea, the Myacea-Pholadacea-Gastrochaenacea, and thirdly in trend 7 where it occurs in the Arcoida and nearly all families of Heterodonta. The independent occurrence of this structure presumably arose by the evolution of similar depositional conditions at the shell-mantle interface, resulting in convergence of depositional morphologies. This convergence is not really all that surprising, for crossed-lamellar structure has also been independently evolved in both the Gastropoda and Scaphopoda.

In a study of various types of nacre, Wise (1970) has attempted to demonstrate an evolutionary significance in his categories 'Vertikalschichtung', 'Treppen', and 'Backsteinbau'. The amount of vertical component in the nacreous structure of the middle shell layers seems to be more closely related to the geometry of the shell, rather than the antiquity of the lineage. Thus bivalves with a low expansion rate (high convexity) will have better developed columnar nacre than forms with a higher expansion rate.

Although this discussion has largely been concerned with the carbonate part of the shell, the shell is of course a two-phased material, the other phase being the organic matrix and both phases have evolved together. Ghiselin *et al.* (1967) and Degens *et al.* (1967) have discussed the phylogeny of the amino-acid composition of the shell matrix proteins in bivalves. Although their conclusions are based upon very limited sampling of taxa, their groupings are generally similar to the shell structure trends recognized here.

Many workers consider the shell matrix to have a very active role in molluscan calcification but, although extensively studied (see Wilbur and Simkiss 1968), the evidence is extremely ambiguous and often based upon preconceived ideas taken

from work on calcification in bone (Glimcher 1960). Recent ideas on the role of the matrix have been well reviewed by Towe (1972). It may be that the matrix has a more passive role in calcification, such as providing a quiet environment, free of Brownian movement, in which crystal nucleation and growth can easily occur. It has been argued that there is a correlation between shell structure type and the composition of the matrix, thereby suggesting a direct control by the matrix on structure (see review, Wilbur and Simkiss 1968). Although to some extent this correlation is true, there are important exceptions. For example, it has been shown by Degens *et al.* (1967), that the shell matrix composition of the Arcacea and Limopacea which have crossed-lamellar shells is more closely similar to that of the Pteriomorphia having foliated and prismatic-nacreous shells, than to other taxa having crossed-lamellar shells. Although it might be argued that different types of matrix can produce the same result, the control would seem to lie in other factors. The evolution of shell matrix composition could possibly be correlated with other factors such as shell strength and thus have a relation with the mode of life and shell structure.

#### HISTORY OF CALCIFICATION IN BIVALVES

Possibly the first calcification in the ancestral molluscs arose as a result of spontaneous precipitation into a mucoid coating lying between the mantle and an outer tanned protein sheet, the periostracum. It is conceivable that those forms with a thicker, more rigid calcified shell were selectively favoured, with a resultant evolution towards a much more heavily calcified shell. In this early state, it is probable that the shell would show no organized structure but consist of an intergrowth of crystals with no particular orientation. Structures such as this are formed by spontaneous precipitation in pulmonate egg shells (into a mucopolysaccharide matrix) (Taylor, unpub.) and in some foraminifera (Towe and Cifelli 1967, pl. 98). Structures almost identical to these can be produced inorganically by growing crystals in gels, by methods similar to those of Henisch (1970). From this early state, how might the most 'primitive' structure we have recognized, simple prisms and nacre in the Monoplacophora, have arisen? By analogy with the metallurgical example described above it is suggested that an increase in calcium carbonate saturation, an increase in crystallization rate, or an increase in impurity (protein) could have collectively or singly produced the spontaneous precipitation of the cellular, polygonal structure of simple prisms. Further from the mantle margin an increased crystallization rate or an increased saturation resulted in the breakdown of the cellular structure to form laminar dendrites (nacre). This cell/dendrite combination may have originally appeared spontaneously, but possibly because of some selective advantage conferred upon the animal became fixed in the population as prisms and nacre. Further elaboration of shell structures mainly concerned the modifications of dendritic growth in the middle layer and the loss of the outer prisms. Thus both foliated and crossed-lamellar structures are regarded as varieties of dendritic growth which have been elaborated from nacreous structure. The mechanisms by which they have arisen are, however, unknown.

The modifications of shell structure could have arisen spontaneously in a section

of the population and subsequently become fixed in a lineage as a result of some selective advantage. This advantage could be a more efficient calcification mechanism involving closer control by the animal. The change from aragonitic to calcitic prisms and from aragonitic nacre to calcitic foliated structure could have originally arisen as a result of colder environmental temperatures, calcite being easier to precipitate in colder water. Or perhaps slight biochemical differences in the extrapallial fluid may be sufficient to cause the precipitation of the more stable polymorph (Wilbur and Simkiss 1968).

Although a relation of shell structure with phylogeny is evident, it has been shown (Taylor and Layman 1972) that there is a strong correlation between structure and the mode of life of the animal concerned. It can thus be argued that the shell structure combinations have been evolved in response to functional demands, although the selective advantages conferred are in most cases unknown. In common with other anatomical characters of the Bivalvia, shell structures exhibit a mosaic evolution. In different phylogenetic lineages various shell structural combinations are evolved at different rates presumably in response to increasing specialization to various diverse modes of life.

Many of the conclusions reached in this paper are speculative, but in view of the paucity of well-preserved shell structure material in the lower Palaeozoic we must rely upon circumstantial or indirect evidence to reconstruct the original radiation pattern of the shell structure combinations.

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